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THE PROTOZOAN LIFE CYCLE.[1]

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Twenty years ago it was an amusing pastime to see with the aid of the microscope, and to describe, new and interesting forms of unicellular organisms. Today there is not a field of biological science that is not illumined by the deeper study of the protozoa, and the pastime of our fathers has become the science of protozoology to-day. In its modern aspect this new science has many sides, morphology, physiology, psychology, cytology, and pathology, and although there is little danger of its being cut up into unrecognizable parts, there is need of some ground principle or principles to hold the many branches of protozoa study together and to unify the science. It was the genius of Schaudinn, whose untimely death has taken from protozoölogy its most brilliant light, to establish such an unifying foundation, and in his clear perception of the importance of the life cycle we have the key note of our present day conception of the protozoa. With our present knowledge we may define protozoa as: Independent, unicellular, animal organisms which reproduce by division or spore formation, the progeny passing through various phases of activity collectively known as the life cycle, and manifesting various degrees of vitality with accompanying form changes.

In thus emphasizing the life cycle in the definition I would seek to introduce into protozoa study the recognition of the entire cycle of changes as a necessary basis for species. I would have the presentation of the life history of a protozoön a prerequisite for its acceptance as a new species and would have zoölogists recog-

[1] Substance of addresses given before Sections D and K of the British Association for the Advancement of Science, at York, 1906

nize that a new species can no more be created on the basis of a single cell or group of cells in the same stage of the life cycle than a species of mammal can be established on the basis of a fore limb, a jaw bone, or a tooth. It seems to me high time that the science of protozoa-study should be freed from the charge of dilettantism, and time for the literature to be cleared of the great burden of synonyms that must ever increase so long as novices in this field of study see and describe in print what to them are new and curious forms.

There is enough known at the present time of protozoan life cycles to indicate that for a given species the cycle under similar conditions is always the same, and we are justified in considering the entire congeries of forms which the protozoön passes through in its life cycle, and not the single cell, as the "individual," comparable indeed, as has long since been pointed out, to the metazoön. There is nothing fanciful in comparing the rapid asexual phase of a protozoön with the proliferation of somatic cells of a metazoön, or the periods of conjugation and old age in a life cycle with the sexual maturity and senescence in metazoa. So many different forms are assumed by the protozoön in the numerous stages of vitality, that, unless the entire cycle is known, even the skilled observer might be justified in considering the various phases of the same organism as different organisms. Instances of this confusion come to your minds at once, and I need but mention Plasmodium and Polymitus, Coccidium and Eimeria to illustrate my meaning. The same confusion has recently come under my observation in connection with *Paramecium aurelia* and *P. caudatum*, which, since the classical work of Maupas, have been generally but erroneously accepted as distinct species.

The specific differences between these two supposedly different forms have been emphasized by Maupas and Hertwig, and more recently by Simpson, and are based upon some minor characteristics of size and form but mainly upon the presence of two micronuclei in *P. aurelia* and one in *P. caudatum*. In all cultures of *P. caudatum*, epidemics of conjugation appear at more or less regular intervals. Four pairs of conjugating forms were isolated from such a culture on March 11, 1905, and after separation the eight individuals were isolated and their several histories followed

out until the race in each case became extinct. Two of the eight individuals representing different pairs continued to multiply in cultures for more than a year, the method employed being the same as that used in previous experiments.[1] The other six died before reaching the fourth generation. One of the two successful exconjugants reorganized as *Paramecium aurelia*, the others as *P. caudatum*. The *caudatum* form was much more vigorous than the *aurelia* form and kept up in its division rate with a ninth individual that was chosen for control from the individuals that had not conjugated in the original culture. At the end of two months the *aurelia* form had divided 55 times, the *caudatum* form 76 and the control 77 times. In the period between the last of April and the end of June the *aurelia* form gradually lost its specific *aurelia* characters and became more and more like *caudatum*. The two micronuclei were reduced to one, one being absorbed, and by the seventieth generation the original *aurelia* form could not be distinguished morphologically from the original *caudatum* form, while its division energy became much greater than that of the other types in culture, an energy which lasted through more than 300 generations.

Without entering into a discussion of the interesting biological features of this apparent change of species which I have published elsewhere,[2] I would merely call attention to the fact that here at any time, during the first 45 generations at least, the thousands of cells that might have been formed would have been classified as *P. aurelia*, while study of the life history shows that it is only a temporary form assumed by *P. caudatum* and is to be interpreted as a mere variant or sport. These results merely emphasize the importance of studying the entire life cycle as a basis for protozoan species.

It is particularly important that these specific distinctions should be clearly recognized in that field of protozoan research which is most important at the present time, — the pathogenic. Here more than in any other field of biological study is the need

[1] Calkins, "Studies on the Life History of Protozoa," I., *Arch. f. Entwk.*, XV., No. 1, 1902.

[2] *Paramecium aurelia and Paramecium caudatum*, in "Biological Studies" by the pupils of William Thompson Sedgwick, Chicago, 1906.

of a clear conception of the different phases of the parasite, and the possibility of different hosts or of different effects on the same hosts at different periods of vitality should be known to the pathologists. The tendency to put protozoa on the same basis of research as the bacteria, despite the brilliant work in cultivating certain types of protozoa on artificial media, which one of my countrymen regards as the *sine qua non* of pathogenic protozoan research, seems to me to be a step in the wrong direction. To study parasitic protozoa in culture is to study them under one condition only, and in one phase only of the life history, and the different forms that are met with in such artificial media may be more often involution types than normal phases, and the great multiplication of species of *Trypanosoma* or *Spirochæta* bespeaks perhaps more than any other one thing the presence of a new type of novitiate in protozoan research.

If the life cycle is to be accepted as the basis of new species, and regarded as the individual in a taxonomic sense, it should be sufficiently definite to be taken as a unit, and the life histories of widely separated species should have some common grounds for comparison. Thanks to the great stimulus given in recent years to protozoan study, we know the full life history of many widely separated forms, and at the present time we are able to generalize to some extent and to formulate a few ground principles. The old-time comparison of the metazoön with the mass of cells that are formed by the repeated division of the first parent cell of a protozoön after conjugation, can be amplified and extended at the present time to the comparison with the metazoön of not only the mass or morphology, but the physiology or general biology of the constituent cells as well. As with the metazoön so with the aggregate of protozoa cells, we note a period of youth characterized by active cell-proliferation; this in both groups of organisms is followed by the gradual loss of the division energy accompanied by morphological changes in type of the cells preliminary to conjugation and fertilization and to the renewal of vitality by this means. When such renewal is omitted, and for one reason or another this stage is never reached by the great majority of protozoa, the third characteristic period — old age — supervenes and the race of pro-

tozoa dies out from protoplasmic senility no less surely than does the body of the metazoön. We can distinguish, then, in the life history of a protozoön three more or less clearly marked stages, youth, adolescence, and old age, each with certain characteristics but which we cannot sharply mark off one from another any more than we can clearly limit the three stages of a metazoön.

As with the fertilized egg of a metazoön, the copula or fertilized cell of a protozoön is endowed with a great power of cell-reproduction and with a high potential of vitality, and this is the main characteristic of the first period of the life cycle. This reproduction may take the form of simple division, of budding, or of spore formation, according to the difficulties that have been successfully overcome by the species in its struggle for existence. The young forms show well marked conformity to type, and this feature, occurring when the greatest numbers of representatives of the species are in evidence, undoubtedly has given a false impression of the stability of form of the protozoan species.

This is the period also of the greatest resistance to adverse conditions of the surrounding medium and in pathogenic forms it is the period of greatest malignancy. It is a well-known fact that, in many parasitic forms of protozoa, attempts to inoculate from animal to animal are either failures altogether or result in a weakened race of the organisms; these failures are perhaps due to the inability of the organisms in a more or less weakened condition to withstand the natural immunity of the host, which they are perfectly able to do with the full potential of vitality with which they are endowed after conjugation. In some cases, as for example in Trypanosoma, the natural vitality of the parasite is so much greater than the natural resistance of the host that such inoculation is possible and the transplanted organisms continue to live. The matter of malignancy is so intimately connected with this question of restored vitality that, in yellow fever for example, it alone is almost sufficient to indicate that conjugation processes must take place in the body of *Stegomyia fasciata.*

This first period is then marked by a distinct excess of constructive over destructive metabolism and in the series of divisions or repeated spore formation which follows fertilization there is a

gradual tendency for the energy of multiplication to weaken, or, as we may express it, the constructive and destructive processes tend to equalize. With the decline of the division rate comes the advent of the second period in which the most important functions in the life of the protozoön occur.

The main characteristic of this second general period, or adolescence, is a general decline in the multiplication rate and more or less definite change in form of the cells and in their chemical and physical composition. A single cell, unless it is in the sexual phase, gives little or no clue to its stage in the life history. In the majority of cases it is only by the study of a long series that the student is able to recognize this period in the life cycle. In such a study, which one can easily carry on with certain free forms of ciliates, the decline of the division rate with advancing age of the series is easily followed. In a form like Paramecium, for example, where there is no sexual dimorphism, one notes at this period a change in the physical constitution of the protoplasm. Such changes, leading in Paramecium to what I have termed the "miscible" state, are certainly the most striking features in the life history of protozoa and *a fortiori* of the period of adolescence, for in them we find an explanation of all the form changes that take place in any life history. Such form changes may involve only the cytoplasm as in *Paramecium* or *Tetramitus*, only the nucleus as in *chromidium* formation in rhizopods, or both nucleus and cytoplasm as in gamete formation with or without sexual differentiation.

In *Paramecium* this condition comes at a period which Maupas designated as sexual maturity. The body size is somewhat less than at earlier periods, although this is by no means a constant feature, size depending chiefly on the rate of division and so only indirectly on age. The plasticity at this period is remarkable, and the cortical plasm is so sticky that two organisms striking each other will fuse at the point of contact. I have had *Paramecia* in culture during an epidemic of conjugation with the protoplasm so highly miscible that amorphous groups of partially fused *Paramecia* were formed by the accidental union of from three to nine individuals, dozens of such groups whirling round and round amongst the normally conjugating pairs.

In *Tetramitus*, *Cercomonas*, or other similar flagellates with a firm contour and a definite shape, the organisms in the period of adolescence become plastic or even amœboid, and like *Paramecium* they conjugate while in this condition.

Among the morphological changes that occur during this period of adolescence none are more subtle or more difficult to interpret than those of the nucleus; indeed, we are here brought face to face with one of the fundamental problems of modern biology — the maturation phenomena. While these are undoubtedly general biology or cell problems, there is another phenomenon connected with the nucleus of protozoa at this period which, despite the ingenious analogies of Goldschmidt, has no satisfactory simulacrum in metazoa, — the formation of *chromidia*. Using the term *idiochromidium* proposed by Mesnil to designate the distributed chromatin prior to gamete formation, we see in this material a practically characteristic sexual substance which, appearing prior to conjugation, belongs primarily to this period of adolescence. In all those forms in which multiple fragmentation has been described, the fragments become the nuclei of conjugating gametes (examples in *Coccidium schubergi* and *Entamœba* according to Schaudinn). In rhizopods, however, especially in the testacea, this nuclear distribution begins at an earlier period in the life history, and the *idiochromidium* is characteristic of the ordinary vegetative forms (examples in *Difflugia* [Zueltzer], *Centropyxis* [Schaudinn], etc.). This chromatin differentiation and distribution indicates a curious change in the chemical balance of nucleus and cytoplasm during the period of adolescence; a change which may appear earlier or later in different types, the earliest appearance being seen in the case of infusoria where the differentiation into vegetative and germinal nuclei occurs immediately after conjugation. In the majority of cases, however, the appearance of the *idiochromidium* and the various stages leading up to its formation may be taken as evidence of advancing age of the series of individuals and as a token of the near completion of the cycle.

So widespread is this nuclear phenomenon and so well established in protozoa studies that we are justified in some cases in arguing from this phenomenon alone that adolescence and the

period of sexual union is imminent. For example, in the case of the ordinary forms of *Amœba* it is remarkable that sexual processes have never been observed, although the engulfing of one individual by another has been interpreted as a conjugation phenomenon. One series of forms has recently come to my notice which seems to indicate a sexual process. The ordinary form of *A. proteus*, usually has but a single nucleus, but in one culture in my laboratory after a long series of uninucleated forms a culture appeared in which the individuals were in various phases of encystment or in nuclear fragmentation immediately prior to encystment. It was found that the single primary nucleus divides by mitosis; that these divide again and so on until as many as seventy large nuclei may fill the body of the amœba. In some cases before this number is reached the larger nuclei begin to break down into large granules which become distributed throughout the cell appearing exactly like the idiochromidium of *Difflugia*, *Arcella* or *Centropyxis*. All but one of the primary nuclei are finally disposed of in this way, that one remaining unused even in the final encysted stage. In this final stage the cyst is filled with many reproductive bodies, which from analogy with other rhizopods I interpreted as gametes.

Not only is chromidium formation important in determining the phase of development of a given form, but it may also be of the greatest assistance in proving the protozoön nature of questionable structures found in certain diseased tissues. An interesting example has recently come up in connection with the organism of rabies. This organism, under the name of the Negri bodies, has been looked upon with great suspicion by biologists and pathologists alike, and from its general staining reaction and from its ordinary vesiculated appearance it has been more frequently passed by as an artifact or secretion or degeneration product, than considered as an organism. But during the season just passed, Dr. A. W. Williams, of New York, working with a different method from that ordinarily employed, was able to prove that what appear usually as vesicles in these bodies are in reality substances which take a characteristic nucleus stain with the Giemsa method, and she shows that the Negri bodies are amœboid cells with nuclei in different stages of chromidium

formation. These erstwhile questionable bodies must now go into the protozoan literature under the generic name of *Neuroryctes* given by Dr. Williams. When the same method comes to be applied to the small-pox organism, I am confident that the last doubter will be convinced that it, too, is a protozoön, and of the rhizopod type.

Still another feature of this second period is the change in form of the conjugating individuals. We have seen that, with increasing maturity, the organisms of a cycle lose their definite shape, become plastic or amœboid in some cases and conjugate while in this condition. Now it is probably due to the same underlying causes that gametes of relatively minute size are formed. In *Polytoma*, for example, size differences are entirely facultative, two normals, two reduced individuals, or one normal and one reduced individual may unite. From such an indifferent condition we find all intermediate stages to fully established obligatory differences in size between conjugating forms and vegetative forms. This might be interpreted as a purely physiological matter depending upon the general chemical and physical balance in the cell, but with it is bound up very often a second phenomenon,—sexual differentiation, which has a deeper significance than the mere change of form at this period of adolescence. The study of protozoa has thrown no light as yet on this problem, which according to recent experimental and cytological findings, especially Wilson's discoveries on the extra sex-determining chromosome in certain insects, would seem to be a matter of inheritance rather than of controllable physiological balance. In many cases what may be called secondary sexual characters in protozoa are evident from the very outset after conjugation, even the first progeny being sexually differentiated as in *Trypanosoma* or *Adelea*, and this certainly can not be traced to advancing age or to changes in chemical relations of nucleus and cytoplasm.

In some cases these differentiations are not established until some change in external conditions brings them out. Klebs, Dangeard, and others have made different types of flagellates conjugate by changing the temperature or increasing the density in the surrounding medium. The same experiment is performed by mosquitoes and other insects on various parasitic

protozoa, as when some blood dwelling parasite is withdrawn from the hot environment of the mammalian body to the colder regions of a mosquito's digestive tract. If such experiments become obligatory, and it is apparently so in many cases, then certainly the most efficient prophylaxis is getting rid of the all-important intermediate host, a preventive measure that has been so signally successful in the Roman Champagna, in Cuba, in Vera Cruz, and in New Orleans.

The happenings within the body of such intermediate hosts are by far the most important to the parasitic protozoa of all their life processes, for the conjugation period with them, as with all free-living protozoa, is the critical period of the life history, and on it depends whether the race shall be given a new vigor and a new lease of life, or shall pass on into the third period of the life cycle characterized by old age or senescence and death.

The third period in the life cycle of protozoa is characterized by the peculiar cytolytic processes that accompany starvation, by loss in size, by vacuolar degeneration in nucleus and cytoplasm, and by final natural death. The symptoms may precede both physiological and germinal death, and many of the so-called involution forms frequently described in parasitic protozoa may be individuals in this third stage of vitality. At this period, conjugation, as pointed out by Maupas, seems to be impossible, the chance of rejuvenescence is cut off, and the race, now comparable to the worn out somatic cells of a metazoön, becomes extinct.

This series of changes from the fertilized cell to the ultimate extinction by natural death is a consecutive series and forms a clean-cut and well-defined life cycle or unit for all forms of protozoa. The vital processes are vegetative in nature and varying phases may be largely accounted for by the conditions of metabolism. In metazoa we can make a clear distinction between the history of the individual and the history of the race, and in protozoa, with the life cycle as the unit, we can make the same distinction. The ordinary phenomena of vegetative life of the cell, metabolism in all its processes, have to do with digestion, excretion, irritability, growth, and multiplication, and are functions pertaining distinctly to the life cycle and may be considered independently of those which have to do with the continuity of the

species or race. Among the latter are the many processes accompanying fertilization and rejuvenescence, and the phenomena here, although not a part of the life cycle any more than sexual processes are a part of the life history of an individual metazoön, are nevertheless dependent on it and can not be omitted in any adequate account of a life cycle, since the succession of cycles, or the race, depends upon them. It is in this field of phenomena that we find the most fascinating aspects of modern protozoa study, for the problems here are general biological problems, and their solution means the illumination of some of the darkest places in biological science. Let me ask your attention for a few minutes, in concluding, to some features of this general subject that have interested me during the past year. They relate to maturation phenomena, to renewal of vitality after conjugation, and to artificial rejuvenescence in *Paramecium*, all functions of the species or race rather than of the unit life cycle.

One of the deepest problems of general biology, heredity, is bound up with the history of the chromatin in the formation of germ cells, and here in protozoa, as the culminating phenomena of the period of adolescence, we find the same type of maturation as in metazoa or the higher plants. At the present time there seems to be no connection whatsoever between the phenomenon of chromidium formation and maturation, while the residual masses of chromatin that are left to degenerate and disappear in so many protozoa prior to fertilization, are more nearly comparable with the residual chromatin of a germinal vesicle in a metazoön than with maturation of the chromosomes. When the history of the idiochromidium is more perfectly established, we may have further evidence to support the identity of the processes in protozoa and metazoa. The division of the chromidium granules in *Amœba proteus* [1] which I have elsewhere described in some detail may be the equivalent of the maturation divisions of the chromosomes in germ cells of the metazoa. There is more definite evidence of this similarity in other forms of protozoa. In *Trypanosoma noctuæ*, for example, maturation processes entirely similar to those of the higher animals have been de-

[1] "Evidence of a Sexual Phase in the Life Cycle of *Amœba proteus*," *Arch. f. Protist.*, Bd. V., 1904.

scribed by Schaudinn. In his preliminary paper this brilliant observer does not go into the details of the process but states categorically that the male nucleus contains only four of the typical eight somatic chromosomes, while the female nucleus contains a similar four in the shape of tetrads formed by the transverse division into four parts of a longitudinally split spireme thread, which are reduced to four single chromosomes by two successive divisions, one a reducing the other an equation division. Cytologists everywhere are waiting for a confirmation and for a more definite description of this remarkable process which thus resembles very closely the maturation processes of certain metazoa. Other instances of reduction in protozoa have been given from time to time, and are quite sufficient to show that maturation phenomena are as widespread in protozoa as in other forms of life and that their underlying significance is as wide as the entire field of biology. The infusoria perhaps more than other forms of protozoa are generally cited in this connection. Here Maupas early showed that of the divisions of the micronucleus of *Paramecium caudatum* one persists to form the functional male and female pronuclei, while the other three atrophy and disappear in the cytoplasm. Schaudinn showed that in Heliozoa one daughter-nucleus which he compared with a polar body is thrown off to disintegrate and disappear in conjugating Actinophrys, while Hertwig showed that two such bodies are cast off by conjugating individuals of Actinosphærium.

In none of these cases has the finer details of chromosome formation been sufficiently described, and the number of chromosomes has rarely been counted or the actual reduction made out. Hertwig somewhat doubtfully claimed that the number in *Paramecium* is reduced from eight or nine to four or six, but there certainly must have been a mistake in the interpretation of what constitutes the chromosome in this case, for the actual number is many times greater than what he gives. One of the graduate students at Columbia, Miss Cull, has worked with me the past year on the formation of the chromosomes during the conjugation period of *P. caudatum*, and although our results on the maturation divisions are not yet ready for publication, we have proved that the history of the chromatin in the early period

of the maturation process agrees with a remarkable exactness with what occurs in many germ cells. The curious and enigmatic crescent which the micronucleus forms during the early phases of maturation, is the form assumed by the nucleus during the stages of synapsis and contraction, and the first spindle develops from this crescentic nucleus with its longitudinally divided chromosomes in the form of heterotypical loops. The condensed chromatin of the resting nucleus is first broken up into many fine granules which become arranged in lines radiating backwards from the intranuclear division center. The nucleus elongates in the direction of these lines until it is seven or eight times the original length. Then, with the growth of the division center, the entire structure becomes crescent shaped and many times the volume of the original micronucleus. The long lines of chromatin appear to form a confused network, but in the contraction phase which follows shortly after the crescent, it can be seen that these lines of chromatin are much thicker than they were and distinctly double, and although not conclusively demonstrated, the most reasonable interpretation regarding their origin is that the long lines of chromatin unite side by side in a typical parasynapsis.

It has been customary to describe the pronuclei in *Paramecium* as fusing while in the spindle form. In a general way this is true, but it is only an elongated form assumed by the nucleus at the time of this union, for the spindle at this time is in no sense a mitotic spindle, the chromatin being in a finely divided state and distributed throughout the nuclei.

It has been generally believed that conjugation brings about a renewal of vitality, a Verjüngung or rejeunissement according to Bütschli and Maupas, or an Erfrischung, to use a term suggested by Weismann. This interpretation seems to be so obvious on *a priori* grounds that experiments to prove it would appear hardly necessary. In protozoa it is not rajuvenescence strictly speaking but the formation of a new individual, and so also is it in metazoa. It would seem to be easy enough to prove that conjugation actually starts a new race from weakened individuals, but singularly few experiments have been undertaken with this object in view. Some that have been carried out by Miss Cull

and myself during the last year, while proving that conjugation does bring about renewed vigor, also show that the interpretation must be trimmed of some of its generalizations.

It has also been generally assumed in cases of conjugation where, as in *Paramecium*, both individuals are similar in size, and where conjugation is only temporary, that both individuals are fertilized, but according to these experiments which I have cited Miss Cull has shown that, in the majority of cases, while one individual of the original pair is markedly vigorous after conjugation, the other one either forms a weak strain or dies off at an early period.

It would seem from these results that in cases like this of isogamous conjugation we can catch a glimpse at least of the same principle that operates in the fertilization of an egg by a spermatozoön, where one cell loses its identity and continues to exist only in conjunction with another cell. It appears to be a case of incipient fertilization and indicates some physiological difference between the conjugating individuals analogous to that between spermatozoön and egg.

The analysis of the conditions governing conjugation has not yet been carried very far. My own experiments show that Maupas's three conditions can not hold. Hunger apparently has nothing to do with it, and diverse ancestry is not essential, for I have obtained as large a percentage of successful endogamous as exogamous pairings and have carried one endogamous exconjugant through 379 generations. Maturity, however, the third "condition" postulated by Maupas, seems to be necessary, understanding by this term the peculiar state of cytoplasm and nucleus when conjugation is possible and a condition which can be induced by artificial means such as change in temperature or of density in the surrounding medium.

There is yet another matter that I wish to speak of in connection with conjugation and rejuvenescence, and that is the question of artificial rejuvenescence, a matter which has an important bearing, it seems to me, in all protozoan life histories. In a series of experiments which I carried on for twenty-three months with one race of *Paramecium*, it was found that periodic reductions of vitality occurred at intervals of about six months. At such

periods of "depression" the race under cultivation would have died out entirely, had not stimuli in the form of extracts of different substances (beef, pancreas, brain, etc.) been applied. With the aid of such restoratives on three different occasions, the race was carried through four "cycles" of activity and through 742 generations.

There is no doubt that the organisms would have died of a real physiological exhaustion, had they not been artificially stimulated, and even when the race finally ran out, it was not from physiological exhaustion in the same sense, for stimuli had again been successful in restoring the vegetative functions. It was due to some more deeply lying trouble, and the results confirmed Hertwig's view of "germinal" death as contrasted with "physiological" death, and, as I have elsewhere pointed out, they demonstrate that in the protozoön as in the metazoön we may distinguish between somatic and germinal protoplasm.

We can readily understand how such periods of depression may be overcome in nature and stimulation effected by changes in the immediate environment or, in parasitic forms, by changes in the blood, and continued activity of certain parasites or appearance of the recidive in malaria, etc., may thus be accounted for. But the organisms themselves have an efficient means of bringing about this renewal of vitality. It seems probable that some original supply of physiological energy is continually drawn upon by the vegetative organisms, some "potential of vitality," which, like the charge of a battery, may become exhausted. As in a battery this potential can be renewed by artificial means, but unlike a battery it can also charge itself by the process of parthenogenesis. This has been shown by Schaudinn to take place in the malaria organism, *Plasmodium vivax* and in *Trypanosoma noctuæ* of the owl. Here, as in some insects, rejuvenescence is brought about by the union of the kinetonucleus and the vegetative nucleus, and is quite analogous to the fertilization in some metazoa of the egg nucleus by a polar body nucleus. Protozoan organisms which are thus restored by parthenogenesis seem to carry with them at least one extra charge of vitality, and we have no basis for speculating as to the length of time that such parthenogenetic processes may continue in a race. In the experi-

mental work on Paramecium artificial parthenogenesis was successful at three different periods of depression but failed on the fourth, and we may infer that normal parthenogenesis has only a limited success and that sooner or later the race must come to an end unless conjugation and nuclear reorganization take place. It is conceivable that parthenogenesis is only a means of offsetting physiological death or in other words, of stimulating physiological activities in protoplasm in which the potential of development is not yet exhausted.

LOCOMOTION IN YOUNG COLONIES OF PECTINATELLA MAGNIFICA.

ALICE W. WILCOX.

Pectinatella magnifica is the largest of the fresh-water bryozoa (Phylactolæmata). It is a distinctively American form and is generally known by the conspicuously large masses of it, which are formed in the late summer and fall. These masses commonly are as large as a man's head and often attain the size of sixteen by eight or nine inches. They are found floating or attached to submerged solid material in some of our purest fresh-water ponds and reservoirs. Each of these masses consists of a thin coating of *Pectinatella* colonies attached to a thick substratum of transparent, colorless jelly. The colonies are diamond-shaped in general form, with many slender, radiating lobes, each bordered by a double row of actively-contracting polypides.

These jelly masses are one of the most unique phases of the life-history of the species. In order to understand their mode of formation, I undertook a preliminary study of the growth and behavior of the young *Pectinatella* colonies. This resulted in the discovery that during their early stages these colonies have the power of independent motion. This paper gives the evidence of this fact of *locomotion in young Pectinatella colonies.*

It was long believed that the power of locomotion in the bryozoa was confined to the genus *Cristatella*, of which it is a striking characteristic. But a Danish zoölogist, Wesenburg-Lund ('96), discovered that another genus of the Phylactolæmata, *Lophopus*, has this power of independent locomotion. He observed that the young *Lophopus* colonies sometimes migrate six centimeters in the course of twelve hours.

In 1901 I studied young colonies of *Pectinatella magnifica* under most favorable conditions at Cold Spring Harbor, L. I. There *Pectinatella* occurs in abundance in three connecting fresh-water ponds. Flood-gates separate the adjacent ponds and to these the statoblasts of *Pectinatella* often attach themselves and

give rise to young colonies. The colonies on one gate I observed regularly at twenty-four hour intervals for a period of six weeks from June 8 to July 21. The observations were recorded in a series of forty-three outline drawings made to scale, showing the colonies in their actual position in relation to certain fixed lines. A selected series of fifteen of these figures is reproduced to illustrate this paper.

In each figure, the unbroken outlines represent the position of the colonies on the date indicated, and the broken outlines their position the previous day. The two straight lines, crossing each other at right angles represent the fixed reference lines on the flood-gate.

Fig. 1 represents two small colonies, *A* and *B*. Colony *A* has just come out of its statoblast and become attached. Colony *B* is somewhat older and about three times as large as *A*.

Fig. 2 represents the same colonies two days later. Their size is not perceptibly increased, but both colonies have moved to the right and *A* has approached a little nearer to *B*. *B* shows a slight constriction preliminary to division.

Fig. 3 represents colonies, *A* and *B*, after another interval of three days. Both colonies have increased in size and are coming still nearer together. *B* is becoming definitely lobed.

Fig. 4 represents the conditions one day later. Colony *A* has migrated back toward its original position. Colony *B* has divided by fission into two parts, B^1 and B^2.

Fig. 5 represents the colonies the following day. Colony *A* is still shifting its position slightly, but without increasing in size. Colonies, B^1 and B^2, are already beginning to move apart and to change their position in relation to colony *A*.

Fig. 6 represents the conditions seven days later. After a period of comparative rest colony *A* has moved to a new position and increased in size. Colonies, B^1 and B^2, are still changing their absolute and relative positions.

Fig. 7 represents the colonies three days later. Each has definitely enlarged and changed its position somewhat. B^2 has moved entirely off its position of the day before as shown by comparing the even and broken outlines of the colony.

Fig. 8 represents the conditions after another interval of three

days. It shows further increase in size and a greater degree of locomotion of each of the colonies.

Fig. 9 represents the colonies three days after Fig. 8. Marked changes have occurred; colony A has more than doubled its size and has divided into two parts: A^1 and A^2, each of which is moving; A^1 is growing and migrating; B^2 has just divided into two parts: $B^{2.1}$ and $B^{2.2}$.

Fig. 10 represents the colonies two days after Fig. 9. They are in a state of rapid growth as indicated by their increased size and their definitely-lobed margins.

Fig. 11 represents the colonies two days later, indicating important changes. Colony A^1 is divided into two: $A^{1.1}$ and $A^{1.2}$, which are moving apart. Colony A^2 is much enlarged and divided into $A^{2.1}$ and $A^{2.2}$. Colony B^1 has become deeply lobed. Colony $B^{2.1}$ is moving and preparing to divide. Colony $B^{2.2}$ has divided into colonies $B^{2.2.1}$ and $B^{2.2.2}$.

Fig. 12 represents the conditions three days later. It shows increase in size of each of the colonies, and further division of colonies $A^{2.1}$, $A^{2.2}$, B^1 and $B^{2.1}$. Also a part of colony $B^{2.2}$ has fused with a part of colony $A^{2.2}$. From this time forward the locomotion of the individual colonies cannot keep pace with their growth. Hence as the colonies divide and move apart they come in contact with other colonies with which they fuse.

Fig. 13 represents the colonies two days after Fig. 12. A number of the colonies are literally running together.

Fig. 14 represents the conditions after an interval of three days. It shows marked growth in every direction. All but a few outlying colonies are united in a single mass.

Fig. 15 represents the colonies three days later. They are forming one continuous mass, which is not only expanding its area rapidly, but also is thickening perceptibly, especially in the middle. The latter change is due to the heaping up of the secretion of the under surface of the colonies.

This study of the young *Pectinatella* colonies shows very conclusively that they possess the power of *locomotion*. This power is definitely associated with the phenomena of growth and division. The increasing size of a colony causes it to divide. The fact that young *Pectinatella* colonies multiply by fission was first

brought out by Hyatt (65). The frequent division of the colonies along with the tendency toward further growth occasions locomotion.

The real cause of locomotion must however be referred back to the activity of the moving colonies and the condition of the substratum on which they rest. The individual polypides of *Pectinatella* are very irritable. They contract and expand frequently and with some force. All the polypides on one side of a colony contracting simultaneously give impetus enough to move the whole colony over a slippery surface. The gelatinous secretion which underlies the young colonies has not yet hardened, and in its semi-fluid state offers a slimy surface over which the small colonies move with very little resistance.

The rate and amount of locomotion varies with the size and condition of the colony. After a colony is well started and growing rapidly, it divides often and the resulting colonies move apart quickly and as far as the free space about them permits. But there are limits to this power of locomotion. The colonies can move only as they are impelled by the activity of the polypides. Hence as the polypides lose their vigor, as they do during reproduction, locomotion must cease. The power of locomotion also decreases with the increasing size of the colonies. The external conditions also limit locomotion. So long as the gelatinous substratum is in a semi-liquid state, the young colonies move with freedom, but as it gradually solidifies they become fixed. Often locomotion is limited also by the space about the colony. If two colonies in process of locomotion come in contact with each other, their motion is checked and they fuse together. As the colonies spread and form a confluent mass, further growth is allowed for only by the rapid thickening of the gelatinous ectocyst.

But what is gained by this unique power of locomotion? As division is necessary to keep the individual colonies small, so locomotion after division, is necessary to allow growth to proceed freely in all directions, and the characteristic radiately-lobed colonies to be formed.

This discovery of locomotion is significant, owing to the light which it throws upon the mode of development of the large

fall masses of *Pectinatella magnifica* already referred to. The only theory of their origin, on record up to this time, is that of Hyatt ('65), who believed that each mass was derived from as many statoblasts as there are colonies. In the light of this study, it is evident that each mass arises from relatively few, instead of innumerable statoblasts, and that it is formed in a similar way to the mass resulting from the two colonies, *A* and *B*, that is, through the combined phenomena of growth, division and locomotion.

BROWN UNIVERSITY,
ANATOMICAL LABORATORY, June, 1906.

LITERATURE CITED.

Leidy, J.
'51 Proceedings of the Academy of Natural Science of Philadelphia, Vol. V.

Hyatt, A.
'65 Observations on Polyzoa. Proc. of Essex Institute, Vol. IV.

Allman, G. J.
'65 Monograph of Freshwater Polyzoa. Ray Society, London.

Allman, G. J.
'79 On the Structure and Development of the Phylactolæmatous Polyzoa. Journ. of Linnean Society, Vol. 14.

Cuvier, G.
'90 Observations sur la Cristatella mucedo. Bull. et Memoirs de la Société Zoologique de France.

Wesenburg-Lund,
'96 Biologiske Studier over Ferskvandebryozoer. Med. 4 tasl. Vid. Meddel. Naturhist. Foren. Kjobenli. (5) 8 Aarg.
Recherches biologiques sur les Bryozoaires d'eau douce. (Résumé en francais) Ibid.

Description of Plates.

Plate VIII.

Fig. 1 represents *Pectinatella magnifica*, colonies: *A*, *B*. July 8.
Fig. 2 represents *Pectinatella magnifica*, colonies: *A*, *B*. July 10.
Fig. 3 represents *Pectinatella magnifica*, colonies: *A*, *B*. July 13.
Fig. 4 represents *Pectinatella magnifica*, colonies: *A*, B^1, B^2. July 14.
Fig. 5 represents *Pectinatella magnifica*, colonies: *A*, B^1, B^2. July 15.
Fig. 6 represents *Pectinatella magnifica*, colonies: *A*, B^1, B^2. July 22.
Fig. 7 represents *Pectinatella magnifica*, colonies: *A*, B^1, B^2. July 25.
Fig. 8 represents *Pectinatella magnifica*, colonies: *A*, B^1, B^2. July 28.
Fig. 9 represents *Pectinatella magnifica*, colonies: A^1, A^2, B^1, $B^{2\cdot1}$, $B^{2\cdot2}$. August 1.

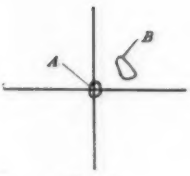


FIG. 1.

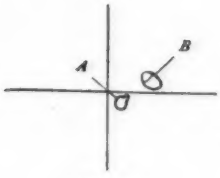


FIG. 2.

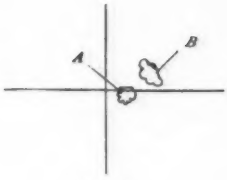


FIG. 3.

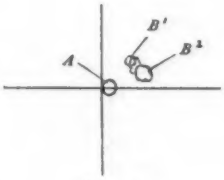


FIG. 4.

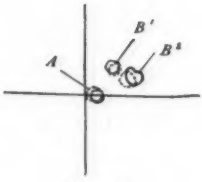


FIG. 5.

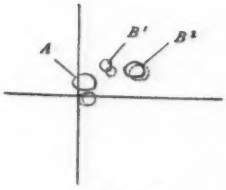


FIG. 6.

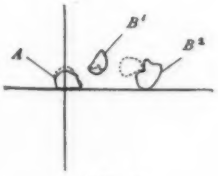


FIG. 7.

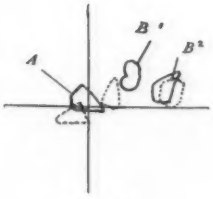


FIG. 8.

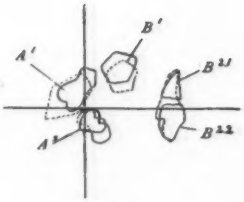


FIG. 9.

PLATE IX.

Fig. 10 represents *Pectinatella magnifica*, colonies: A^1, A^2, B^1, $B^{2\cdot1}$, $B^{2\cdot2}$, August 3.

Fig. 11 represents *Pectinatella magnifica*, colonies: $A^{1\cdot1}$, $A^{1\cdot2}$, $A^{2\cdot1}$, $A^{2\cdot2}$, B^1, $B^{2\cdot1}$, $B^{2\cdot2\cdot1}$, $B^{2\cdot2\cdot2}$. August 5.

Fig. 12 represents *Pectinatella magnifica*, colonies: $A^{1\cdot1}$, $A^{1\cdot2}$, $A^{2\cdot1\cdot1}$, $A^{2\cdot1\cdot2}$, $A^{2\cdot2\cdot1\cdot1}$, $A^{2\cdot2\cdot1\cdot2}$, $A^{2\cdot2\cdot2}$, $B^{1\cdot1}$, $B^{1\cdot2\cdot1}$, $B^{1\cdot2\cdot2}$, $B^{2\cdot1\cdot1}$, $B^{2\cdot1\cdot2}$, $B^{2\cdot2\cdot1}$, $B^{2\cdot2\cdot2}$. August 8.

Fig. 13 represents the same colonies as Fig. 12 fusing. August 10.

Fig. 14 represents the same colonies as Fig. 12 fusing. August 13.

Fig. 15 represents the same colonies as Fig. 12 fusing. August 16.

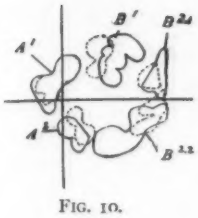
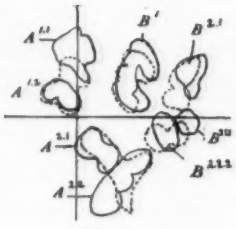


FIG. 10.



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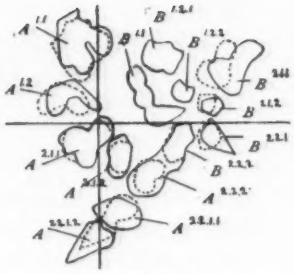

FIG. 12.

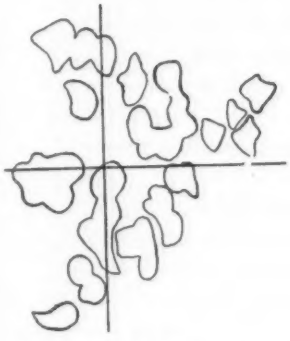

FIG. 13.

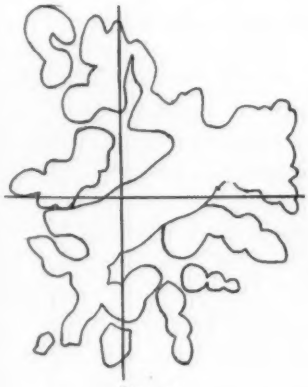

FIG. 14.

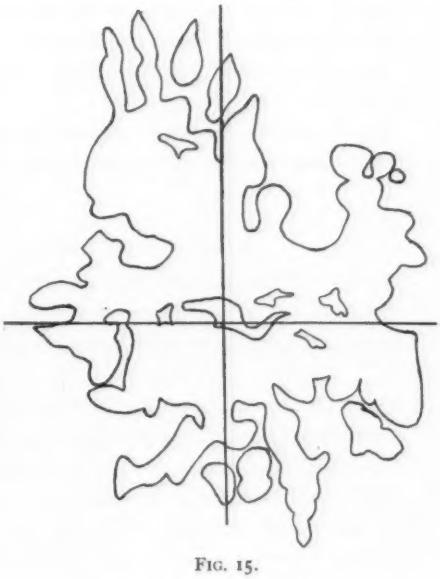

FIG. 15.

ON THE RELATIVE DIMENSIONS OF THE OSSEOUS SEMICIRCULAR CANALS OF BIRDS.[1]

MAY AGNES HOPKINS.

The purpose of this paper has been to determine whether there is any relation of the comparative dimensions of the bony semicircular canals of the ear of birds, either to mode of locomotion, or to genetic affinities.

These precise questions have apparently not been considered, except in a short paper by Farrar (1831) that was inaccessible to me. Indeed there has been no extended comparative study of the dimensions of these bony canals, though the inner ear labyrinth has been carefully investigated, notably by Retzius (1884).

In all cases my dissections were made on dried adult skulls. The material used was the collection of the University of Texas. All the American specimens studied had been identified by Prof. Montgomery, and exotic ones by the dealers from whom they were secured.

The work was done entirely under the direction of Prof. Montgomery, to whom I am greatly indebted for his valuable assistance and encouraging sympathy.

1. MODES OF LOCOMOTION IN BIRDS.

Archæopteryx, the earliest known bird, was a good flyer if we may judge from its possession of a sternal keel, but it also used its fore-limbs as grasping organs since they were provided with free unguiculate digits.

What has given birds their superiority over the reptiles was the acquisition of flight, and the main avian peculiarities are referable to this mode of locomotion. Birds may have developed flight in one of two ways — by saltatory locomotion, whereby the hind limbs were used as propellers, and the fore-limbs as organs of balance; or by scansorial locomotion on trees, whereby

[1] Contributions from the Zoölogical Laboratory of the University of Texas, No. 74.

the fore-limbs came to be used as parachutes in the aerial passage from one tree to another. The second of these ways may have been the more probable. No modern birds use their wings in the manner of legs, except the young of *Opisthocomus*, but employ them rather as organs of flight, as balancers or as flippers (penguins).

The different modes of locomotion are intimately connected. In this study of the bearing of the relation of the size of the semicircular canals to the mode of locomotion, the following main kinds of locomotion were distinguished: The *cursorial*, where the hind limbs are employed to the greatest extent, and upon the hard ground; of such birds I have examined the ostrich and roadrunner. The *arboreal*, where wings and feet are employed about equally, as in most of the passeres. A modification of the preceding is the *scansorial* locomotion of such birds as woodpeckers. The *volant*, where the wings are used to the greatest extent, as in all birds of long sustained flight; those with the power of soaring represent the acme of this mode of locomotion. The combination of *volant* and *nektant*, that is of strong flight with the power of swimming, as in the gulls and albatrosses. The *pygopodal*, which may be swimming under water (grebes), or flight under the water (penguins). The *grallatorial*, where the birds walk upon moist or yielding ground, with an elongation or partial webbing of the toes; such birds have either a strong or weak power of flight and some of them can swim to a slight extent.

In the evolution of these modes of locomotion a climbing, arboreal habit was probably earliest. From this would have followed divergently: (*a*) development of stronger flight, and more aerial life; (*b*) loss of flight and terrestrial running; (*c*) development of a wading habit. Swimming birds have probably descended from waders and divers from swimmers. The most modified birds, from the standpoint of locomotion, would be the two very different groups of flightless birds, the Ratitæ and the Sphenisci.

In any study of genetic relationships of birds one may find some help in considering the evolution of modes of locomotion.

2. Dimensions of the Canals.

The right ear was the one studied in all cases, and the semicircular canals laid bare by the knife. To measure these curved canals a piece of No. 50 cotton thread was drawn around each and the length marked on it; then the exact length of the thread when straightened out was ascertained. All absolute dimensions are stated in millimeters. All measurements were made twice, at an interval of time, in order to secure the greatest possible accuracy. For units of comparison a median vertical and a median basilar cranial length were employed. The vertical length is the distance from the ventral face of the occipital condyle to the large transverse muscle crest immediately above the foramen magnum; the basilar length is the distance from the posterior face of the condyle to the anterior aperture of the Eustachian tube as marked by bony ridges. These were taken as units of comparison because they can be very accurately measured, but especially because they are lengths of parts of the skull that are perhaps the least subject to variation.

In the tables the first three vertical columns give the absolute lengths of the semicircular canals. The fourth and fifth columns give the absolute basilar and vertical lengths of the skull for comparison. The succeeding three columns show which of the canals are largest. The ninth column gives as the "combined measurement" of comparison the sum of the vertical and basilar cranial lengths divided by two. The tenth column expresses the sum of the absolute lengths of all three canals. And the last column represents this sum divided by the combined cranial measurement given in the ninth column. This last column, accordingly, states the sum of the lengths of the three canals in relation to a definite length of the skull, and may be called the "relative total length."

A comparison of the figures given in the last column of the tables shows what genera have the relatively larger, and what ones the relatively smaller canals, expressed in terms of the cranial measurements. We find then the following associations according to this relative sum total length of the canals:

1.00 mm. to 1.25 mm., the one genus *Pelecanus*.

1.25 mm, to 1.49 mm., *Struthio*, and certain Anatidæ (*Anas*).

Family and Genus.	Length of Anterior.	Length of Posterior.	Length of Exterior.	Basal Measurement.	Vertical Measurement.	Posterior Largest.	Exterior Largest.	Exterior and Posterior Equal.	Combined Measurement.	Sum of Three Canals.	Relative Total Length.
Struthionidæ.											
Struthio camelus Linn.	32	18	14	43	43	×			43	64	1.49
Spheniscidæ.											
Eudytes minor	18	13	11	23	26	×			24	42	1.75
Phalacrocoracidæ.											
Phalacrocorax mexicanus (Brandt.)	12	9	10	16	18		×		17	31	1.82
Pelecanidæ.											
Pelecanus erythrorhynchus Gmel.	17	11	11	31	35			×	33	39	1.18
Ardeidæ.											
Ardea herodias Linn.	19	12	13	18	19		×		18	44	2.44
" *rufescens* Gmel.	12	10	10	15	14			×	14	32	2.28
" " "	15	9	10	15	15		×		15	35	2.33
" " "	12	8	9	12	11.9		×		12	29	2.41
Nycticorax nycticorax nævius (Bodd.)	15	12	13	16	16		×		16	40	2.49
Ciconiidæ.											
Ciconia (? C. alba.)	21	13	12	28	27	×			27	46	1.70
Anatidæ.											
Dafila acuta (Linn.)	11	9	10	19	18		×		18	30	1.66
Aythya americana (Eyt.)	12	9	10	20	20		×		20	31	1.55
Anas boschas Linn.	12	10	9	23	23	×			23	31	1.43
Chen hyperborea (Pall.)	15	8	10	21	20		×		20	33	1.65
Nettion carolinensis (Gmel.)	9	6	7	15	14		×		14	22	1.57
Anser albifrons gambeli (Hartl.)	13	10	10	20	21			×	20	33	1.65
" " " "	13	10	10	20	21			×	20	33	1.65
Querquedula discors (Linn.)	10	7	8	14	14		×		14	25	1.78
Cathartidæ.											
Catharista urubu (Vieill.)	20	11	12	20	23		×		21	43	2.04
Cathartes aura (Linn.)	17	12	12	18	18			×	18	41	2.27
Falconidæ.											
Buteo borealis (Gmel.)	21	17	15	18	20	×			19	53	2.78
Falco columbarius Linn.	15	12	12	10	15			×	12	39	3.25

Family and Genus.	Length of Anterior.	Length of Posterior.	Length of Exterior.	Basal Measurement.	Vertical Measurement.	Posterior Largest.	Exterior Largest.	Exterior and Posterior Equal.	Combined Measurement.	Sum of Three Canals.	Relative Total Length.
Tinamidæ.											
Tinamus brasiliensis	15	11	10	16	12	×			14	36	2.57
Tetraonidæ.											
Colinus virginianus (Linn.)	10	8	9	12	10		×		11	27	2.45
" " "	10	7	8	10	8		×		9	25	2.77
Callipepla squamata (Vig.)	10	7	8	9	9		×		9	25	2.77
" " "	10	7	8	10	9		×		9	25	2.77
" " "	10	7	8	10	9		×		9	25	2.77
Cyrtonyx montezumæ mearnsi (Nels.)	11	9	9	12	9			×	10	29	2.90
Phasianidæ.											
Meleagris gallopavo Linn.	17	13	11	22	21	×			21	41	1.99
Gallus bankiva Linn.	14	12	10	18	10	×			17	36	2.11
Rallidæ.											
Fulica americana Gmel.	14	9	10	14	13		×		13	33	2.53
Rallus	13	9	10	14	13		×		13	32	2.46
Porzana	11	6	7	9	8		×		8	24	3.00
Gruidæ.											
Grus mexicana (Müll.)	18	11	12	19	20		×		19	41	2.15
Charadriidæ.											
Squatarola squatarola (Linn.)	16	10	11	11	12		×		11	37	3.36
" " "	13	10	11	11	12		×		11	34	3.09
Charadrius	12	9	9	9	10			×	9	30	3.33
Ægialitis wilsonia (Ord)	8	7	6	8	9	×			8	21	2.62
Ægialitis vocifera (Linn.)	9	7	7	10	9			×	9	23	2.77
Scolopacidæ.											
Numenius longirostris Wils.	13	8	8	9	10			×	9	29	3.22
Gallinago delicata (Ord.)	13	8	8	9	10			×	9	29	3.22
Tringa maculata (Vieill.)	9	6	7	8	8		×		8	22	2.75
Tringa bairdii (Coues)	9	5	6	9	8		×		8	20	2.50
Ereunetes pusillus (Linn.)	8	5	6	7	6		×		6	19	3.16
" " "	8	5	6	7	6		×		6	19	3.16

Family and Genus.	Length of Anterior.	Length of Posterior.	Length of Exterior.	Basal Measurement.	Vertical Measurement.	Posterior Largest.	Exterior Largest.	Exterior and Posterior Equal.	Combined Measurement.	Sum of Three Canals.	Relative Total Length.
Scolopacidæ.—*Continued.*											
Calidris arenaria (Linn.)	8	6	6	7	7			×	7	20	2.85
Totanus melanoleucus (Gmel.)	12	8	9	11	10		×		10	29	2.90
Totanus flavipes (Gmel.)	11	7	8	9	8		×		8	26	3.25
Symphemia semipalmata inornata (Brewst.)	13	9	9	12	11			×	11	31	2.81
Aphrizidæ.											
Arenaria morinella (Linn.)	11	8	7	9	10	×			9	26	2.88
Laridæ.											
Larus atricilla Linn	16	8	7.5	13	12.3	×			13	31	2 38
Larus delawarensis Ord	15	9	8	14	12	×			13	32	2 46
Sterna maxima Bodd	14	10	8	15	17	×			16	32	2 00
Stercorariidæ.											
Stercorarius longicaudus (Vieill.)	14	10	9	13	14	×			13	33	2.53
Columbidæ.											
Columba fasciata (Say)	14	9	10	12	13		×		12	33	2.91
Columba ænas	14	9	8	12	11	×			11	31	2.81
Turtur auritus	12	7	6	10	9	×			9	25	2.77
Zenaidura macroura (Linn.)	10	6	7	9	9		×		9	23	2.66
Cuculidæ.											
Geococcyx californianus (Less.)	18	8	11.5	14	13		×		13	31	2.84
Psittacidæ.											
Psittacus erythacus	13	10	10	17	15			×	16	33	2.06
Alcedinidæ.											
Ceryle alcyon (Linn.)	13	10	9	12	13	×			12	32	2.66
Strigidæ.											
Strix nyctea Linn	23	18	15	18	17	×			17	56	3.29
Bubonidæ.											
? *Asio accipitrinus* (Pall.)	15	12	11	15	14	×			14	38	2.71
Caprimulgidæ.											
Phalænoptilus nuttallii nitidus (Brewst.)	11	6	7	9	8		×		8	24	3.00
Chordeiles virginianus (Gmel.)	11	8	8	9	10			×	9	27	3.00

Family and Genus.	Length of Anterior.	Length of Posterior.	Length of Exterior.	Basal Measurement.	Vertical Measurement.	Posterior Largest.	Exterior Largest.	Exterior and Posterior Equal.	Combined Measurement.	Sum of Three Canals.	Relative Total Length.
Caprimulgidæ.—*Continued.*											
Chordeiles acutipennis texensis (Lawr.)	11	8	8	8	9			×	8	27	3.37
Trochilidæ.											
Trochilus colubris (Linn.)	5	4	4	3.8	3			×	3	13	4.33
Picidæ.											
Dryobates villosus harrisi (Aud.)	10	8	9	10	11		×		10	27	2.70
Dryobates pubescens (Linn.)	9	7	7	9	8			×	8	23	2.87
Dryobates scalaris bairdi (Malh.)	10	8	8	9	10			×	9	26	2.88
Melanerpes erythrocephalus (Linn.)	12	9	10	9	10		×		9	31	3.44
Colaptes auratus luteus Bangs.	13	10	12	13	12		×		12	35	2.91
Tyrannidæ.											
Myiarchus cinerascens (Lawr.)	9	6	7	9	9		×		9	22	2.44
Corvidæ.											
Corvus americanus Aud.	16	11	13	14	15		×		14	40	2.92
Icteridæ.											
Molothrus ater Bodd.	9	6	7	7	7		×		7	22	3.14
Sturnella magna hoopesi Stone	10	6	8	10	10		×		10	24	2.00
Fringillidæ											
Amphispiza bilineata deserticola (Ridgw.)	7	5	6	6	6		×		6	18	3.00
Tanagridæ.											
Piranga rubra (Linn.)	9	7	7	8	8			×	8	23	2.87
Hirundinidæ.											
Progne subis (Linn.)	9	6	5	9	9	×			9	20	2.22
Mniotiltidæ.											
Dendroica coronata (Linn.)	8	4	5	6	6		×		6	17	2.83
Troglodytidæ.											
Galeoscoptes carolinensis (Linn.)	9	6	7	9	9		×		9	22	2.44
Paridæ.											
Parus atricristatus (Cass.)	8	6	6	8	8			×	8	20	2.50
Turdidæ.											
Merula migratoria (Linn.)	10	7	8	9	9		×		9	25	2.77

1.50 mm. to 1.74 mm., the families Ciconiidæ, Anatidæ (*Dafila, Aythya, Chen, Nettion, Anser*).

1.75 mm. to 1.99 mm., the families Spheniscidæ, Phalacrocoracidæ, and Anatidæ (*Querquedula*).

2.00 mm. to 2.22 mm., the families Carthartidæ (*Cartharista*), Gruidæ, Phasianidæ, Laridæ (*Sterna*), Psittacidæ.

2.23 mm. to 2.46 mm., the families Ardeidæ (*Ardea*), Cathartidæ (*Carthartes*), Tetraonidæ (*Colinus*), Laridæ (*Larus*), Tyrannidæ, Hirundinidæ and Troglodytidæ.

2.47 mm. to 2.70 mm., the families Ardeidæ (*Nycticorax*), Tinamidæ, Rallidæ (*Fulica, Rallus*), Charadriidæ (*Ægialites*), Scolapacidæ (*Tringa*), Stercorariidæ, Columbidæ (*Zenaidura*), Alcedinidæ and Paridæ.

2.71 mm. to 2.94 mm., the families Falconidæ (*Buteo*), Picidæ (*Dryobates, Colaptes*), Tetraonidæ (*Colinus, Callipepla, Cyrtonyx*), Charadriidæ (*Ægialites*), Turdidæ, Scolapacidæ (*Tringa, Calidris, Totanus, Symphemia*), Aphrizidæ, Columbidæ (*Columba, Turtur*), Mniotiltidæ, Cuculidæ and Tanagridæ.

2.95 mm. to 3.18 mm., the families Rallidæ (*Porzana*), Charadriidæ (*Squatarola*), Scolapacidæ (*Ereunetes*), Icteridæ, Caprimulgidæ (*Phalænoptilus, Chordeiles*), and Fringillidæ.

3.18 mm. to 3.32 mm., the families Falconidæ (*Falco*), Strigidæ and Scolopacidæ (*Numenius, Gallinago*).

3.32 mm. to 3.56 mm., the families Charadriidæ (*Squatarola, Charadrius*), Caprimulgidæ (*Chordeiles*) and Picidæ (*Melanerpes*).

4.33 mm., the family Trochilidæ.

These data show that birds of the most diverse forms of locomotion, and of very diverse affinities may show the same relative sizes of semicircular canals. For example an excellent flyer, the black vulture (*Cathartista*), and the poor flyers, the chicken (*Gallus*) and the parrots (Psittacidæ), have the same relative measurement, 1.98 mm. to 2.22 mm. Further, in certain families the genera may exhibit great differences in these measurements, as particularly in the Charadriidæ and Anatidæ.

The relative sizes of the three semicircular canals to each other may be summed up as follows:

The anterior canal is always the largest.

The posterior canal is larger than the exterior in all the follow-

ing families: Struthionidæ, Spheniscidæ, Ciconiidæ, Tinamidæ, Phasianidæ, Aphrizidæ, Laridæ, Strigidæ, Stercorariidæ, Alcedinidæ, Bubonidæ, and Hirundinidæ.

The exterior canal is larger than the posterior canal in the families: Phalacrocoracidæ, Cuculidæ, Tyrannidæ, Corvidæ, Icteridæ, Fringillidæ, Mniotiltidæ, Troglodytidæ, and Turdidæ.

The posterior and exterior canals are equal in the families: Pelecanidæ, Tanagridæ, and Paridæ.

The posterior canal is larger than the exterior, or the posterior and exterior canals are equal, in the family Falconidæ.

The exterior canal is larger than the posterior canal, or the exterior and posterior canals are equal, in the families; Ardeidæ, Cathartidæ, Tetraonidæ, Caprimulgidæ, and Picidæ.

Falling under none of the above groups are the families: Anatidæ, Charadriidæ, Scolapacidæ, and Columbidæ; in each of which there are great generic differences of the relative sizes of the canals.

3. Types of Canals.

In taking the measurements of the canals, I noticed that the position of the canals with reference to one another or the angle at which they are joined, was not always the same. There are

Fig. 1. Fig. 2. Fig. 3. Fig. 4. Fig. 5.

five types, though these intergrade, under which all species may be grouped (Figs. 1–5). It will be noticed that these are differences mainly of the anterior canal, depending on its length.

Type I. (Fig. 1), the genera *Struthio* and *Tinamus*.

Type II. (Fig. 2), Cathartidæ, *Geococcyx*, Scolopacidæ, Laridæ, *Stercorarius*, *Columba*, *Zenaidura*, *Ceryle*, Caprimulgidæ, *Strix*, *Asio*, Tetraonidæ.

Intermediate between types III. and V. are the genera *Turtur*, *Melanerpes*, and *Dryobates*.

Type III. (Fig. 3), *Ardea*, *Phalacrocorax*, *Ara*, Anatidæ.

Type IV. (Fig. 4), *Ciconia*, Rallidæ, *Grus*, *Eudytes*, *Psittacus*.

Intermediate between III. and IV. are the genera *Pelecanus*, and *Meleagris*.

Type V. (Fig. 5), *Falco*, Charadriidæ, *Colaptes*, *Trochilus*, and the Passeres.

In the above, as in the results from the comparison of the measurements, the types of canals bear no relation to locomotion; for different genera having very different modes of locomotion have the same type of canal; for example in type II. occurs *Catharista*, one of the best flyers, and in the same group *Geococcyx* which seldom flies but is one of the ablest runners.

4. Eustachian Tube Apertures.

The Eustachian tubes have a common œsophageal opening in all cases, except in the genera *Struthio*, *Eudytes* and *Tinamus*, where there is a pair of apertures.

The Eustachian tube is a perfect bony tube in the following: *Sterna*, *Squatarola*, *Ceryle*, *Psittacus*, *Geococcyx*, Tetraonidæ, Phasianidæ, *Catharista*, *Falco*, *Eudytes*, and *Tinamus*. In all other cases it is imperfectly ossified.

Conclusions.

From a careful consideration of all the preceding data, the following conclusions may be drawn:

1. The anterior canal is always the largest.

2. The exterior canal is larger than the posterior in the greater number of cases.

3. The relative measurements of the canals to each other, as well as their sums, bear no direct relation to modes of locomotion.

4. Relative dimensions certainly stand in no relation to broader racial affinities and such dimensions can be used as taxonomic characters only to limited extent.

5. What occasions differences in these dimensions remains to be determined.

6. The anterior vertical canal is the one most subject to variation of position.

7. Types of bony labyrinths, distinguished according to relative positions of the canals, appear to stand in no relation to mode of locomotion, but to a certain extent are indicative of genetic affinity.

8. There are two main modes in the position of the pharyngeal aperture of the Eustachian tubes: a common pharyngeal aperture, or two distinct ones.

Bibliography of the Osseous Canals of Birds.

None of the following works, except that of Farrar, bear directly upon the question undertaken by me, but the list is given to show what has been done upon the bony canals.

Breschet, G.
'36 Recherches anatomiques sur l'organe de l'audition chez les oiseaux. Paris.

Deiters, O.
'60 Untersuchungen über die Schnecke der Vögel. Arch. f. Anat. Phys.

Ercolani, G. B.
'43 Ricerche anatomiche sull'organ dell'audito de ale Ucceli. Nuos. Ann. Science natural. di Bologna.

Farrar, W.
'31 On the auditory apparatus in the skulls of quadrupeds and birds as auxiliaries in the classification. Loudon's Magazine Nat. Hist., Vol. 4.

Flourens, P.
'28 Experiences sur les canaux semi-circulares de l'oreille chez les Oiseaux. Ann. Sci. Natur.

Hasse, C.
'71 Zur Morphologie des Labyrinthes der Vögel. Anatomische Studien, herausg. v. Hasse. Zweites Heft.

Pohl, C. E.
'18 Expositio generalis anatomica organi auditus per classes animalium. Dissert. Vindabonæ.

Retzius, G.
'84 Das Gehörorgan der Wirbethiere. Bd. II. Stockholm.

Windischmann, C.
'31 De penitiori auris in Amphibiis structura. Lipsiæ.

LONGEVITY OF A VELVET ANT.

ADELE M. FIELDE.

Finding no printed record concerning length of life in the Mutilidæ, I think there may be value in an observation recently made by me upon a single female of *Spheropthalmia occidentalis*.

She was captured in Arizona early in June, 1905, by Professor Edward S. Morse, of Salem, Mass.; reached my hands on the first day of the ensuing August; and lived under my observation until the twelfth of August, 1906. She was kept by me in a small glass ant-nest of the Fielde pattern, in which I fixed three glass vials whose interior diameter was scarcely greater than that of her own abdomen. Into one of these vials she often crept; and she hibernated there during the winter of 1905–6, at a temperature between 65° and 75° F. Whenever the temperature rose as high as 80° F. she awoke, walked about and perhaps ate from the particle of honeyed sponge-cake that always awaited her in the adjoining compartment of the nest, where there was also a bit of sponge that was kept saturated with clean water. In summer she often sought the more humid part of the nest.

She preferred darkness to light; but, like the formicid ants, she avoided only the ultra-violet rays. When sheltered by an orange pane which excluded the ultra-violet rays, she was manifestly unaware that she was not in complete darkness. Like the formicid ants she appeared to be blind to other than the actinic rays.

When first received by me, she once stung me sharply, but thereafter she became acquainted with my hand, seemed to greatly enjoy walking about upon it, and never left it willingly except to enter her nest.

I never heard her stridulate when in the nest; but whenever I enclosed her in the warm darkness of my fist, she sounded her charming, harmonious notes, representing but two keys. Probably each key was determined by one of the two overlapping sclerites on the top of the abdomen. Great variation in the

rapidity of the muscular contraction produced at different times an effect like that of playing different tunes on a minute stringed instrument. The sound was sometimes audible at a distance of one yard; but it was much more often audible only when the fist inclosing the insect was in contact with the ear. Occasionally she stridulated continuously for as long a time as three or four minutes.

It is probable that this velvet ant lived at least three summers. The tendency to hibernate in a snug, arid cell, at temperatures below 75° F., makes it unlikely that her progenitors had reared her in the summer in which she was captured. She must, then, have been hatched as early as the summer of 1904. Her existence was probably shortened by an unnatural environment. My observation of this specimen therefore indicates that the female of the velvet ant may live several years.

THE DEGENERATE EYES IN THE CUBAN CAVE SHRIMP, PALÆMONETES EIGENMANI HAY.[1]

FRANK H. PIKE.

The blind shrimp whose eyes are considered in this paper is common in the pools of the sink holes and caves near Cañas on the Western Railway of Cuba. The material was collected by Professor C. H. Eigenmann, who described the localities in his account of "The Fresh-water Fishes of Western Cuba" ('03). The species was described by W. P. Hay, in his paper "On a Small Collection of Crustaceans from the Island of Cuba" ('03).

Material. — Four specimens were available for study. The general topographic relations were determined from a surface study of the different specimens. The histological detail was worked out mainly from one series of sections. The normal marine shrimp from Wareham, Mass., was used for comparison.

Methods. — The animals were killed in formalin and transferred to seventy per cent. alcohol. Preparatory to sectioning, the head was cut off and placed in Perenyi's fluid for about twenty-four hours, dehydrated, cleared in xylol, and imbedded in paraffin. Longitudinal horizontal sections were made. They were mounted on the slide by the water method, and stained with hæmalum and eosin. One specimen was killed in Vom Rath's fluid and stained with safranin. The eyes of the normal shrimp were depigmented by being placed in a ten per cent. solution of nitric acid for from twenty-four to seventy-two hours before being placed in Perenyi's fluid. The remainder of the technique was the same as for the degenerate eye.

[1] Contributions from the Zoölogical Laboratory of Indiana University, No. 58. This study was completed many months ago. Its publication has been delayed to secure good photographs of the critical sections. The material was collected with a grant from the Carnegie Institution.

The Gross Anatomy.

General External Appearance. — Like the cave crustaceans of southern Indiana and Kentucky, the Cuban shrimp is clear white or colorless. The antennæ are extremely long and the chelæ are relatively longer than in the out-door or normal species. The eye-stalks are plainly visible but not as prominent as in the normal species. In the cave-crayfish from southern Indiana and Kentucky the eye-stalks are almost hidden beneath the rostrum, when viewed from above. They are much more prominent in the present species.

Surface Views of the Eye-stalks. — I. Viewed from the side, with moderate magnification, the eye-stalks are seen projecting forward from the anterior lateral part of the head just below and to one side of the rostrum (Fig. 1). The eye-stalk is not termi-

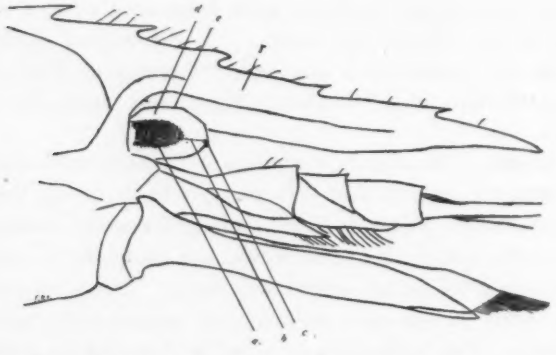

Fig. 1. Eye-stalk viewed from side. *r*, rostrum; *e*, eye-stalk; *a*, optic ganglion; *b*, optic nerve; *c*, retina; *d*, space filled with hæmolymph.

nated by a hemispherical cap as in the normal species, but by a peculiarly shaped, somewhat acute-tipped cone. The stalk is directed upward, forming a small angle with the horizontal. If the line drawn from the middle point of the base through the tip be taken as the long axis of the eye, the part of the stalk above this line will be at all points convex in outline. Beginning at

the tip, the part of the stalk below this line is slightly concave for about one-half the distance from the tip to the base of the cone. From this middle point of the base of the cone on to the base of the stalk, the outline is again convex.

The cuticula is clear white and partially transparent, with no trace of facets in the corneal region. There may be seen through it (*a*) a white mass, very nearly concentric in curvature with the outline of the eye-stalk, extending from the base forward a little more than two-thirds of the distance to the tip of the stalk, and terminating in a blunt cone; (*b*) a find strand running from a point a little below the end of this cone forward to (*c*) a small group of granules in the tip of the stalk. These granules appear to be spread over a small area on the proximal face of the cuticular tip, and taper to a narrower diameter where the thread joins them; (*d*) a space appears between the white mass (*a*) and the cuticula on the sides of the stalk. No trace of pigment is visible with any magnification. In sections these structures are seen to be (1) the optic ganglion, (2) the optic nerve, (3) the remnants of the retina and dioptric apparatus, and (4) a space filled with hæmolymph, respectively.

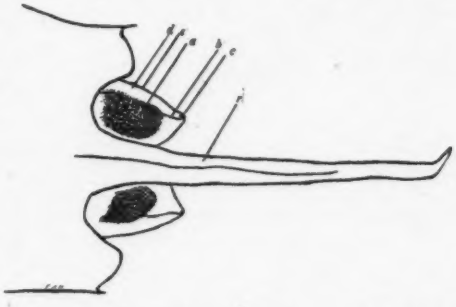

FIG. 2. Eye-stalk viewed from above. *r*, rostrum; *e*, eye-stalk; *a* optic ganglion; *b*, optic nerve; *c*, retina; *d*, space filled with hæmolymph.

Any great amount of shrinkage due to reagents would certainly break the fine strand of fibers running to the granules in the tip. I am inclined, therefore, to believe that the greater part of the space seen between the optic ganglion and the cuticula is normal in this eye.

II. Viewed from above, the outer side of the eye-stalk slopes inward toward the rostrum at an angle of 15 to 20 degrees to the longitudinal axis of the body. (Fig. 2.) The stalk terminates in a blunt, slightly rounded cone. The anterior mesial

edge of the stalk slopes inward and backward to the rostrum. The entire outline of the eye-stalk, when viewed from above, is singularly free from the graceful curvature of the normal eye-stalk. The same structures seen in the side view appear in this view. The tip of the eye-stalk is directed outwards away from the rostrum, and the optic nerve springs from the outer side of the anterior end of the optic ganglion. The granules are applied to the lateral surface of the stalk. The anterior end of the optic ganglion is more rounded than it is in the side view.

General Appearance in Sections. — The specimen on which the account of the minute anatomy here recorded is based, measured 17 mm. in length. The eye-stalk is 1,044 micra in its greatest length and 793 micra in its greatest width. The ratio of the length of the eye-stalk to its width is 1.3. The cuticula of the eye-stalk varies in thickness. It is 14.3 micra thick on the outer side of the stalk away from the rostrum, 10.9 micra in the region where the retinal elements are applied to it, and 7.2 micra on the inner side of the tip next the rostrum.

FIG. 3. Low power microphotograph of eyes of blind shrimp from above. *ct*, corneal cuticula; *c*, retina; *a*, fibrous portion of optic ganglion; *o*, cellular portion of optic ganglion; *h*, hypodermis.

In the left eye, the hypodermis and the retina have adhered to the tip of the stalk, but the optic nerve has broken so that the retina and the optic ganglion are separated. The retina is applied to the side of the eye-stalk. In the right eye, the hypodermis and the retina have pulled loose from the corneal cuticula, but the optic nerve is unbroken. (Fig. 3.)

The optic ganglion appears as a fibrous area surrounded by small cells with large, deeply-staining nuclei. The hypodermis has been torn loose from the sides of the eye-stalk and, in places, lies close to the optic ganglion. Transverse sections of the eyes of a specimen killed in Vom Rath's fluid show the hypodermis lying in contact with the cuticular wall.

In the right eye, a fibrous strand — the optic nerve — extends from the anterior outer part of the ganglion forward to the retinal elements. The optic nerve is bounded on each side by a layer of pavement cells with prominent nuclei. (Fig. 5.) In the right eye, the retinal elements are spread out rather loosely in the form of a fan, the apex of which is directed toward the optic nerve. Some spongy tissue, probably coagulated hæmolymph, appears on each side of the optic nerve between the bounding membrane and the hypodermis.

FIG. 4. Eye of normal shrimp; same magnification as Fig. 3.

Comparison of Normal and Degenerate Eyes. — Fig. 3 is from a photograph of the eyes of the blind shrimp. Fig. 4 is from a photograph of the author's preparation of a normal shrimp eye, made with the same magnification used in Fig. 3. It will be noticed (1) that the degenerate eye is much smaller than the normal eye, (2) that its optic ganglion is apparently a single mass of cells and fibers, and is not divided into parts as in the normal eye, and (3) that the retina and dioptric apparatus are represented by the merest vestiges of these structures as they exist in the normal eye.

Fig. 5. Eye of blind shrimp. 4 mm. objective and 4 projection eye-piece. *rt*, retinula cells; *b*, optic nerve; *mb. l*, bounding membrane of optic nerve; *h*, hypodermis; *ct*; corneal cuticula; *d*, coagulated hæmolymph.

A few numerical results will make these contrasts more evident. There are present in each eye of a normal decapod about 2,500 ommatidia. (Parker, '95). Each ommatidium is composed of sixteen elements: two corneagen cells, four cone cells, two distal retinula cells, one rudimentary and seven functional proximal retinula cells, and one or more accessory pigment cells. In the retina of a normal eye there are, then, about 40,000 cells, about 22,000 of these being retinula cells. There are in the degenerate eye not more than 100 and not less than 50 retinula cells, and not more than ten or twelve cone cells. The cone cells in the normal eye outnumber those in the degenerate eye a thousand to one, and the retinula cells of the normal eye outnumber those of the degenerate eye by at least two hundred to one.

As stated above, the ratio of the length of the eye-stalk to its width in the degenerate eye is 1.3. In a normal crayfish eye I found this ratio to be 1.9. In the eye shown in Fig. 4, this ratio is 1.6. I do not know the range of variation in this ratio in the normal eye, but I feel safe in saying that the degenerate eye has decreased relatively more in length than in width.

The Minute Anatomy.

The Retina in the Left Eye. — The hypodermis consists of oblong cells closely applied to the cuticula and containing relatively large nuclei, Fig. 5. At the extreme tip, the cells become more spherical in shape and are slightly separated from the cuticula. The nuclei are less prominent than in the other hypodermis cells. Beneath these smaller cells is a layer of three somewhat larger spherical cells. Below these occurs a layer of two cells. All have small nuclei and clear cytoplasm. Two irregular masses, staining deeply with hæmalum but exhibiting no discoverable structure, lie, one on each side, immediately beneath the hypodermis and to one side of the clear cells above mentioned. Immediately beneath these dark masses are two other irregular, structureless patches staining diffusely with eosin and not at all with hæmalum.

Miss Seaton ('03) states that, in the compound eyes of Machilis, the cone cells do not stain readily with plasma stains. In some of my own preparations, the cone cells do not stain as readily

with a plasma stain as do some of the other tissues of the eye. Does this consideration, together with the position of these clear cells, afford us sufficient evidence to warrant us in regarding them as degenerate cone cells? I shall presently give a stronger argument in support of this conclusion. What the dark masses and the irregular patches of tissue represent I am not prepared to say. I am not certain that they posses any special morphological significance.

Beneath these structures is a group of larger cells with large, deeply staining nuclei. The nucleus occupies nearly all the space in the cell, there being only a narrow ring of cytoplasm within the cell wall. A plainly marked fibrous tract, the optic nerve, extends from these cells toward the optic ganglion. A fine membrane separates this fiber and cell tract from the hæmolymph or spongy tissue on either side. The large cells are, as I shall presently show, retinula cells.

The Retina in the Right Eye. — The tearing loose of the retina from the cuticula has destroyed the cone cells and the hypodermis at the tip so that no trace of either is visible. The looser arrangement of the large, deeply staining cells permits of a more accurate determination of their relation to the fibers of the optic nerve. With the oil immersion lens, the fibers can be traced up to these cells and can be seen ending in them. (Figs. 6, 7, *n* and *rt.*)

The objection may be urged that, since hæmalum is not a nerve stain, the fibers in question have not been shown to be nerve fibers. The reaction to iron hæmatoxylin is not as marked as in the fibers of the cephalic ganglion, but is still marked enough to indicate that they are nerve fibers. The strongest evidence that they are nerve fibers is their relation to the optic ganglion and their correspondence in position and relation to the nerve fibers in the normal eye. I believe that the simplest explanation open to us is that the fibrous strand represents the optic nerve.

Parker ('95) states that, in the normal decapod (*Astacus*) eye, the fibers of the optic nerve pass through the retinula cells and disappear in the region of the rhabdome. There is no instance known to me in which degeneration has caused a change in the

location of a nerve ending. I consider the deeply staining cells to be degenerate retinula cells. The cone cells have lost their distinctive characteristics much more than the retinula cells.

Summary. — The degenerate eye has a relatively shorter stalk than the normal eye. The corneal cuticula is thinner than that on the outer side of the eye-stalk. The optic ganglion appar-

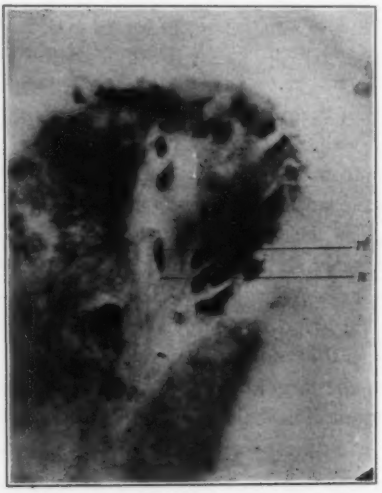

FIG. 6. Eye of blind shrimp. 2 mm. oil immersion objective, 4 projection eye-piece. x 1,000. *rt*, retinula cell in which a nerve fiber, *n*, may be seen to end.

ently consists of a single mass of fibers and cells. There is normally some space between the optic ganglion and the cuticula of the eye-stalk. The optic nerve, extending from the optic ganglion to the retina, is present. The retinula cells, in which the fibers of the optic nerve terminate, still persist. The vestiges of the cone cells may be, and probably are, present. The structures serving to distinguish light from darkness, probably being older phylogenetically than the structures concerned with the production of a definite image, are less degenerate than the latter. The active structures of the eye, represented by the retinula cells, have degenerated vastly more than the passive structures such as the cuticula.

Several questions arise to which no satisfactory answer can at present be given. (1) To what extent has the internal morphology of the neurones of the adult optic ganglion been modified by degeneration? (2) To what extent has the degeneration of the axones affected the cephalic ganglion of the animal? (3) What is the condition of the eyes in the embryo? The neurones of the

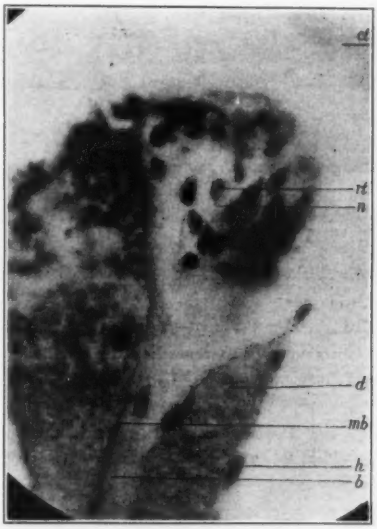

FIG. 7. Same eye as in Fig. 6, but different focus. x 1,000. *n*, a nerve fiber ending in *rt*, a retinula cell; *d*, coagulated hæmolymph; *mb*, bounding membrane of optic nerve; *b*, fiber of optic nerve; *h*, hypodermis; *ct*, corneal cuticula.

Microphotographs by Dr. D. W. Dennis, Earlham College, Richmond, Indiana.

optic ganglion seem to have degenerated so much that their internal morphology is enigmatical. No nuclear wall nor chromatin threads could be seen in any of them, even when stained with iron hæmatoxylin. It is an open question what the phylogeny of the decapod eye has been, and what bearing the present case of degeneration may have on the Law of Biogenesis. The embryological history might throw some light on this latter phase of the question, but it has been impossible so far to find embryos.

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BIBLIOGRAPHY.

Only a partial list is given here. A more complete list is given by Parker, '95.

Carriere, J.

'85 Die Sehorgane der Thiere vergleichend-anatomisch dargestellt.

Eigenmann, C. H.

'03 The Freshwater Fishes of Southwestern Cuba. Bulletin U. S. Fish Commission, 1902, pp. 211–236.

Hay, W. P.

'03 On a Small Collection of Crustaceans from the Island of Cuba. Proceedings U. S. National Museum, Vol. XXVI., pp. 429–435.

Parker, G H.

'90 The Histology and Development of the Eye in the Lobster. Bull. Mus. Comp. Zoöl. at Harvard College, Vol. XX., No. 1.

'90 The Eyes of Blind Crayfishes. Bull. Mus. Comp. Zoöl. at Harvard College, Vol. XX., No 5.

'95 The Retina and Optic Ganglia in Decapods, especially in Astacus. Mittheil. aus der Zoöl. Station Zu Neapel, 12 Band.

Seaton, Frances.

'03 The Compound Eyes of Machilis. Am. Naturalist, Vol. XXXVII., pp. 319.